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THE WING-FINGER OF PTERODACTYLS, WITH RESTORATION OF NYCTOSAURUS

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The question whether the wing-finger of pterodactyls is the fourth or the fifth has been disputed for the past eighty years, though for the past forty years authors have been almost unanimously agreed that it is the fifth. The first writer of credibility who expressed an opinion on the subject was Cuvier, who considered it the fourth. His reasons for so doing, as published in his *Ossemens Fossiles*, are today, I believe, unanswerable, and to him should be given the credit, and not to H. v. Meyer, for the correct recognition of the finger. I quote his remarks in full:

En fin il a ce doigt énormément prolongé en tige grêle, qui caractérise éminemment notre animal.

Il a quatre articulations sans ongle. Le quatrième doigt des lézards aurait cinq articles et un ongle; mais, dans les crocodiles, il n'a que quatre articles, et il est dépourvu d'ongle comme ici; seulement il n'y éprouve pas ce prolongement extraordinaire.

Le crocodile et les lézards ont en outre un cinquième doigt qui dans les, lézards a quatre articles, et dans le crocodile est réduit à trois sans ongle.

Il paraît que dans l'animal fossile il ne reste qu'un vestige de cinquième doigt, mais assez obscur et sujet à contestation.

Le grand doigt est probablement le quatrième, car c'est aussi le quatrième qui est le plus long dans les lézards.

Les trois autres le précédaient dans l'ordre inverse du nombre de leurs articles.

The first author to adopt the other view, that the finger is in reality the fifth, was Goldfuss, who, as Plieninger has shown in his full and reliable review of the subject, thought he saw in the pteroid bone a first finger, accidentally misplaced in his specimen, and in which he thought he recognized an additional phalange even. H. v. Meyer early adopted Goldfuss' view, as shown in the following quotation: "Es zeichnen sich diese Thiere vor allen anderen wirklich dadurch aus, dass der Finger sie zum Fliegen befähigte,

und zwar nur ein Finger, die Ohrfinger, welche wegen der Kleinheit womit er in der Hand anderen Geschöpfe sich darstellt auch der kleine Finger genannt wird" (*Paleontographica* [1851], 19).

But Meyer soon returned to the Cuvierian position, calling the first of the small, clawed fingers the thumb. I can find no independent arguments of Meyer giving the reasons for his views; indeed in various places he is more or less obscure, referring to the "Flugfinger" as the "Ohrfinger," though there can be no doubt but that as early as 1860 he had, as I think, correctly recognized the digit as the fourth. Owen in his *Paleontology and Comparative Anatomy of Vertebrates* figures four small, clawed fingers in front of the wing-finger, which he calls the fifth. Later he reverted to the Cuvierian view. Goldfuss's views were followed by Oscar Fraas and most modern authors, including Marsh, Zittel, Plieninger, and Eaton. In 1904,¹ without at the time having read Cuvier's remarks on the subject, I published a brief article in the London *Geological Magazine* giving reasons for the older view, that the finger is in reality the fourth, as based chiefly upon the recognized normal number of phalanges in the hands of reptiles.

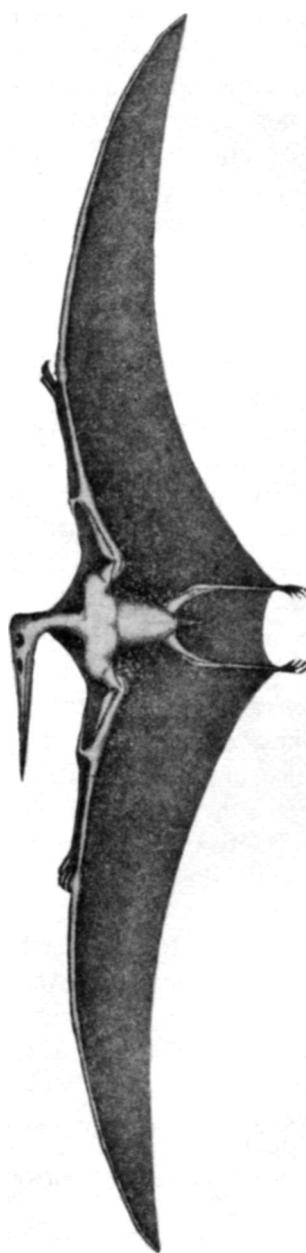


FIG. 1.—Restoration of *Nyctosaurus gracilis* Marsh, by Herrick E. Wilson

¹ "The Fingers of Pterodactyls," *The Geological Magazine*, 1904, p. 59.

Two years later Plieninger¹ discussed the subject fully and well, reaching no positive conclusion, though evidently favoring the Goldfuss view that the finger is the fifth. He showed that Goldfuss, and not Fraas, as I had thought, was the first author to suggest the identification of the pteroid with the first finger, and corrected Seeley's statement that Meyer had so recognized it. We have seen from the quotation that Seeley was really not so far wrong after all, since Meyer did at one time consider the "Flugfinger" as the "Ohrfinger." Finally Abel² in a recent paper has restated the problem, adopting the original Cuvierian view.

As bearing upon this question we have been fortunate in recent years in determining the intimate structure of the hands and feet of several of the early reptiles, from which I may say with entire assurance that, until the close of Carboniferous times, and probably till the close of Permian times, the phalangeal formula for reptiles was the primitive one of 2, 3, 4, 5, 3 for the front feet; 2, 3, 4, 5, 4 for the hind. Plieninger has raised a question in the cited paper whether the formula 2, 3, 4, 4, 3, as seen in the crocodiles, was not really the primitive one for the hands instead of 2, 3, 4, 5, 3, as found in the generality of modern lizards and in *Sphenodon*. In the accompanying figures the front limbs of three of these reptiles, from the so-called Permian of Texas and New Mexico, are shown, made out with certainty in nearly every detail. In Fig. 4 the distal three phalanges of the fourth finger have not yet been positively fixed, but inasmuch as the fourth digit of the hind foot of the skeleton to which the figured hand pertains has definitely five phalanges, there can be no doubt of the number in the same digit of the hand. In Figs. 2 and 4 the bones of the forearm and wrist are shown in a horizontal plane without the foreshortening of the oblique position that they really had in life, and which is shown in Fig. 3. Fig. 2 is that of a cotylosaur, probably belonging in the suborder Pareiasauria, while Figs. 3 and 4, *Ophiacodon*³ and *Var-*

¹ "Ueber die Hand der Pterosaurier," *Centralbl. für Mineralogie, Geol., etc.*, 1906, p 399; also *Paleontographica*, LIII (1907), 301.

² "Die Vorfahren der Vögel," *Verhandl. der K.K. zoologisch-bot. Gesellsch.*, LXI (1911), 163.

³ The full description of this genus will appear shortly in a paper by Dr. Case and the writer.

nosaurus, are zygocrotaphic reptiles that may be included in the order Theromorpha or Pelycosauria.



FIG. 2.—Right front leg of *Limnoscelis* Williston, a corylosaur reptile from the Permian of New Mexico. A little less than one-half natural size.

In all these forms it will be observed that the fifth digit is much reduced, more so than in the hind feet of the same animals. The number of phalanges in this finger in each is three and no more; this is positive. Furthermore it will also be observed that the supporting carpale 5 is reduced or wanting in all; that is, the loss of this bone, the rule in all later reptiles, had begun even before the close of Carboniferous times.¹

It may therefore be assumed with assurance that the ancestors of the pterosaurs had the phalangeal formula for the hand of 2, 3, 4, 5, 3, with the fifth finger much reduced in size and its supporting carpale 5 greatly reduced or entirely lost. In adaptation to aerial flight the pectoral girdle² and front limbs in the pterodactyls have been greatly modified throughout. In *Pteranodon* and *Nyctosaurus*, the most highly specialized, but three carpal bones remain, a proximal one, doubtless the fused radiale, intermedium, and ulnare; a lateral carpal for the support of the pteroid, which may be either the centrale or the first carpale; and a distal one, which in my opinion represents the fourth carpale alone; which, it will be seen, is the largest in reptiles. The carpale bearing the "Flugfinger" is always the larger; in *Pterodactylus* there is another, smaller one in front bearing the anterior metacarpals. I cannot believe that this carpale is the reduced or lost fifth carpale of the ancestral pterosaur carpus, nor that the wing-finger has migrated from its own vestigial carpale to the enlarged fourth while the fourth has migrated to a more anterior carpale. From the carpus then of pterodactyls it would seem highly probable that the carpale is the fourth and that it supports its proper finger the fourth, and not the fifth.

As has been known since the time of Cuvier, the phalangeal formula in pterodactyls, beginning with the first clawed finger, is

¹ I may mention here that evidence is accumulating to prove that the so-called Permian of Texas, or at least its lower part, and of New Mexico, as well as of Illinois, really pertains to the upper part of the Pennsylvanian.

² In my recent work on *American Permian Vertebrates*, p. 58, fourth line from bottom, occurs an unfortunate error, due to the omission of a qualifying phrase, "absent 'among nonamphibious reptiles,'" whereby I say that the supracoracoid foramen is wanting only among Pterosauria, when its absence in the Plesiosauria, most Ichthyosauria, Phytosauria, Chelonia is known to all.

2, 3, 4, 4, to which there are probably few or no exceptions. The first three of these agree absolutely with the normal and primitive formula of the first three digits. The fourth pterodactyl finger has

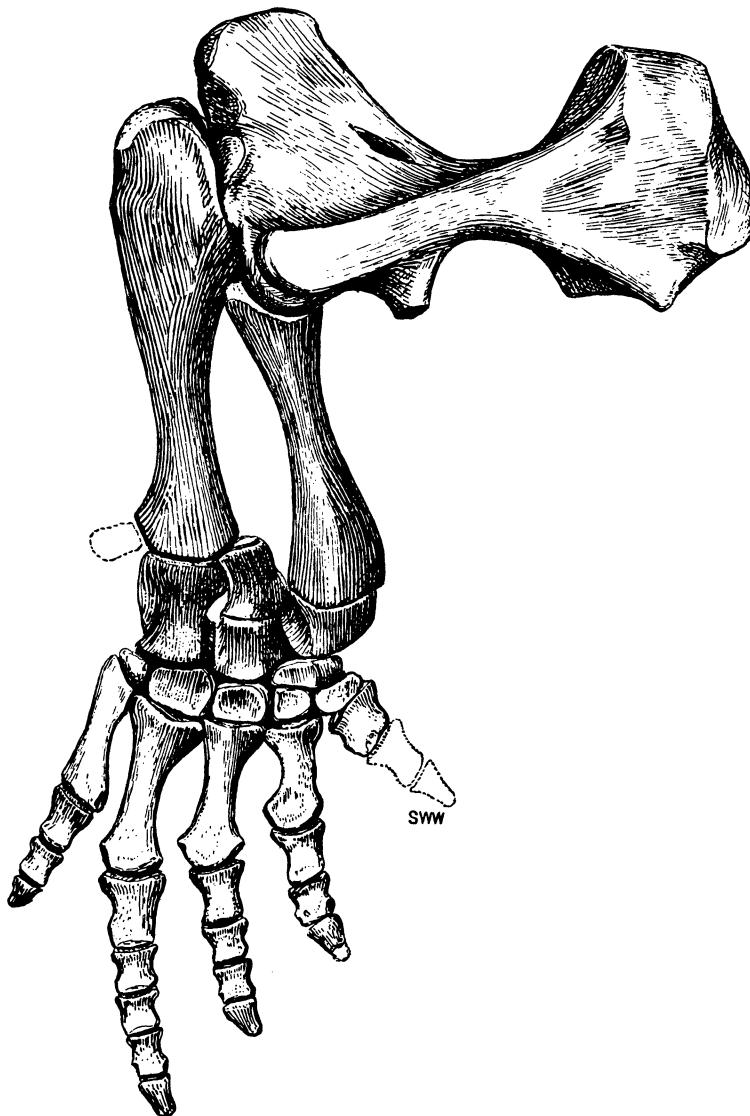


FIG. 3.—Right front leg of *Ophiacodon* Marsh, a theromorph reptile from the Permian of New Mexico. Two-thirds natural size.

but four phalanges, one less than the normal number, and quite that of the crocodiles; that is, as I have previously urged, it lacks the claw. In the acquirement of a membrane-bearing function this is precisely what would be expected in any finger, and is what occurs in the bats, as Abel has said. That the claw gradually elongated, changing its function from prehension to supporting, seems highly improbable. This finger then answers all the requirements for the fourth. If, on the other hand, in consonance with the Goldfuss theory, it is the fifth digit which acquired the membrane-supporting function, not only must the claw have changed its function and become elongated but a new phalange must have been added to the finger. Although among aquatic reptiles hyperphalangy is a common characteristic, we know of no instance among terrestrial vertebrates that I can recall where an additional phalange has been acquired, in either the front or the hind feet. And, if the Goldfuss theory be true, not only must there have been hyperphalangy in the fifth digit, but hypophalangy in the four preceding digits; that is, in the acquirement of a wing function, an increase and loss of phalanges must have occurred concurrently in the hand. I cannot believe that this was the case. Had we not to deal with the peculiar bone called the pteroid, articulating with the carpus and turned backward toward the elbow, the question of the homology of the wing-finger would doubtless never have been raised.

It is the pteroid, then, which has caused all the dispute, from the necessity of accounting for the bone, which, other than a misplaced first metacarpal, seems inexplicable. Two derivations have been imputed to it, as a sinew bone, and as a sesamoid bone. In favor of its being merely an ossified sinew is the fact that, in the remarkable specimen I have described of *Nyctosaurus*, seven well-ossified tendon bones are seen lying by the side of the forearm and hand, elongated bones with one end flattened and the other attenuated. In favor of the latter view that it is merely a sesamoid bone developed in the tendon of some carpal muscle originally is the fact that sesamoid bones do occur elsewhere in the pterodactyls. In the above-mentioned specimen of *Nyctosaurus* I found one lying over the end of the radius and another over the outer end of the coracoid; and I have seen them often in *Pteranodon*. Sesamoid bones have

bursal sacks and synovial joints. That the pteroid bone originated as a tendon or sesamoid bone is quite possible and even probable, but that the bone finally acquired another function, at least in the most highly developed forms, would seem to be very probable. The function that has generally been ascribed to it is that of a "Spannknochen" or tensor of the patagial membrane in front of the elbow. Under the assumed relations of the membrane to the front of the arm I have protested against this theory, since the fact is that there could have been little or no membrane in this region to be rendered tense, provided the membrane terminated, as is usually assumed, at the shoulder. Under the assumption that it really served as a "Spannknochen" I have suggested in an earlier paper that the membrane continued beyond the shoulder along the side of the neck to the skull.

In the accompanying restoration, Mr. Herrick E. Wilson, of the University of Chicago, after careful study, has embodied these views, based upon my skeletal restoration of *Nyctosaurus*. I believe that this restoration comes nearer to the real appearance of a pterodactyl

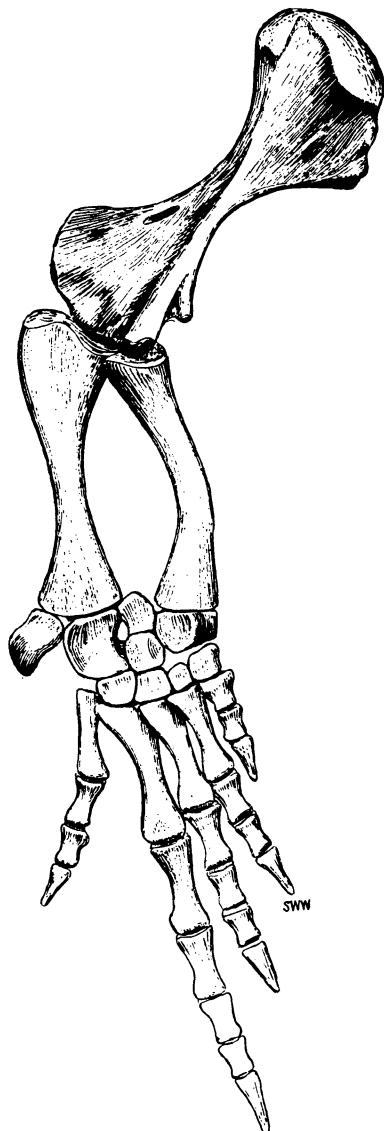


FIG. 4.—Right front leg of *Varanosaurus* Broili, a theromorph reptile from the Permian of Texas. Seven-tenths natural size.

in life than any that has hitherto been published. That the membrane extended on the neck is of course yet a hypothesis based upon the mode of development of the parachute in flying animals of today, and especially upon the structure of the pteroid bone and its relations to the forearm and shoulder. It is a fact that this bone seems to be better developed in *Nyctosaurus* than in other known pterodactyls, reaching by its pointed extremity pretty well toward the shoulder. If it was divaricated from the arm, as its perfect ball-and-socket mode of articulation with the carpus would indicate, and not inclosed in a muscle at its pointed extremity, its function as a supporter of a membrane in front of the elbow can scarcely be taken into consideration. With the membrane extending past the shoulder to the neck it would have had a distinct function as a "Spannknochen" and not otherwise.

Objection may be raised against the wide expanse of membrane between the legs. That the membrane extended to the tarsus on the peroneal side of the legs I think now hardly admits of doubt; the animals would hardly have been "flugfähig" were the legs wholly free, since the wing membrane would have been too narrow to serve as a parachute, and since the legs with their attached membrane must have functioned much like the tail feathers of modern birds in the control of flight. *Rhamphorhynchus gemmingi* has been restored by Zittel without membrane between the legs, but such a condition must seem impossible for such a flying creature. With the wings extended and the membrane connected with the ankles, there must have been a constant and considerable abducting strain on the legs, which must have required a constant muscular tension to withstand; and the legs, in the later pterodactyls at least, seem too frail for such tension. The head of mammals in the horizontal position is kept in place, not by muscular action, which would be unbearable, but by the elastic ligament of the neck. Something like this must have been necessary to withstand the constant abducting tension of the legs of pterodactyls in flight, and I assume that this was the function of a tense membrane between the legs, as well as that of directing flight. It has been suggested that the border of this membrane connected with the end of the vestigial tail; possibly that was the case, but, in *Nyctosaurus* at least, such

an excised membrane would have been little better than none at all.

That the ribs of the abdominal region extended out into the patagial membrane on the sides I have given reasons for elsewhere; I can see no other explanation for their position and lack of curvature in the specimen of *Nyctosaurus* to which I have referred.